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# Wrack burial reduces germination and establishment of the invasive cordgrass *Spartina densiflora*

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## Abstract

Germination and emergence of halophytes may decrease significantly by seed burial in dead plant material, or wrack, which is common and abundant in tidal marshes. The effects of plant debris (wrack) burial on seed germination and seedling establishment of *Spartina densiflora*, an invasive cordgrass, were studied under greenhouse conditions and compared with field observations. Five wrack burial depths were applied: control without wrack, 1 cm (1235 ± 92 g DW wrack $m^{-2}$), 2 cm (3266 ± 13 g DW $m^{-2}$), 4 cm (4213 ± 277 g DW $m^{-2}$), and 8 cm (6138 ± 227 g DW $m^{-2}$). Sediment pH, electrical conductivity, redox potential and temperature were recorded. Quiescence increased with wrack load up to ~20% at 8 cm deep. Germination decreased with wrack load from 96% to 14%, which could be related with anoxic conditions under the debris since sediment redox potential was as low as -83 ± 7 mV at 8 cm. Germination percentage increased and quiescent and dormant percentages decreased at higher daily sediment temperatures and with higher daily temperature fluctuations, conditions that were recorded without or under low loads of wrack. *Spartina densiflora* did not show primary dormancy, but its seeds entered into a non-deep physiological dormancy below 1 cm deep in plant debris. The establishment of *S. densiflora* seedlings was also greatly reduced by wrack burial since only 6 seedlings (11 ± 5 % of germinated seeds) emerged above plant debris from 1 cm and all seedlings died from deeper than 1 cm. *S. densiflora* seedling development was also reduced by wrack burial. The inverse relationship between germination and emergence of *S. densiflora* with wrack burial recorded in our study is useful to predict its invasion dynamics and to plan the management of invaded marshes.

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**Keywords**
Coastal marshes, physiological dormancy, plant debris, seedling, *Spartina densiflora*

## Introduction

Most salt marsh environments are unpredictable for plants, because of the occurrence of both salinity and flooding stress (Cantero et al. 1998). When conditions for seed germination are not favorable, ungerminated seeds of halophytes often remain under enforced dormancy in the soil and serve as a transient or persistent seed bank (Ungar 1995). Thus, seed banks are particularly important in maintaining populations of halophytes in saline marshes (Coteff and Van Auken 2006). Salt marshes are among the most heavily invaded systems in the world (Grosholz 2002). The ability of introduced species to bank seeds can contribute to invasion success, since seeds can persist while waiting for favorable conditions. This ability is especially useful in environments where opportunities for seed germination are infrequent or unpredictable such as salt marshes (Parker et al. 1989). Management of invasive species in salt marshes can be challenging because monitoring and control must continue for at least as long as their seeds persist in the seed bank (Panetta and Timmins 2004).

Rafts of dead plant material, or wrack, are common and abundant in tidal marshes. Due to high primary productivity rates and low consumption rates by herbivorous, halophytes, such as eelgrasses and cordgrasses, produce high quantities of wrack, especially in dye-back areas. This wrack is added up to that transported by rivers to salt marshes in estuaries. Then, tidal creeks provide corridors for wrack transport into salt marshes where it can disturb plant communities (Reidenbaugh and Banta 1980; Bertness and Ellison 1987; Valiela and Rietsma 1995; Tolley and Christian 1999; Brewer et al. 1998; Minchinton 2002). As part of the natural disturbance regime, deposited wrack mats often create bare spots by killing not only the surface vegetation, but also the below-ground biomass (Hartman 1988). Seeds of different salt marsh plants can germinate in the spaces opened by wrack accumulation, playing a key role in plant distribution (Hartman et al. 1983; Pennings and Richards 1998), but germination and emergence may decrease significantly by seed burial in plant debris. Buried seeds are recruited only when they are brought back to the surface by disturbances (Facelli and Pickett 1991). However, these effects are poorly understood since there is a general lack of research that examines the effects of wrack burial in salt marshes.

The austral cordgrass, *Spartina densiflora* Brongn. (Poaceae) is invading salt marshes in southern Europe, Northwest Africa and the West Coast of North America (Bortolus 2006). In invaded marshes, *S. densiflora* develops very dense populations where large amounts of dead matter are deposited (Nieva et al. 2001; Castillo et al. 2008). Moreover, *S. densiflora* seeds float so they are dispersed by currents and tides together with plant debris (Howard and Sytsma 2013). One of the keys to the success of *S. densiflora* invasion is its ability to produce large quantities of viable seeds (Nieva et al. 2001a,b).

*Spartina densiflora* produces many seedlings in intertidal mudflats but its recruitment is very low in marsh zones where wrack is accumulated.

While cordgrasses (*Spartina* genus) are one of the most abundant and frequent halophytes in salt marshes, there have not been any studies that examined how their seeds and seedlings respond to wrack burial. We examined under controlled greenhouse conditions the impact of five wrack burial depths (0, 1, 2, 4 and 8 cm) on germination, seed viability and seedling establishment of *S. densiflora*. Main abiotic factors conditioning seed germination and seedling establishment in salt marshes (sediment pH, electrical conductivity, redox potential and temperature) were also recorded for every wrack treatment. We hypothesized that *S. densiflora* germination and establishment would be reduced by wrack burial due to anoxia and/or low temperature fluctuations.

## Methods

### Seed and wrack collection

*Spartina densiflora* seeds were collected in August 2009 from multiple mature individuals chosen at random from a population growing at the periphery of an accreting, well-drained intertidal lagoon at Odiel Marshes (Southwest Iberian Peninsula; 37°08' - 37°20'N, 6°45' - 7°02'W; Fig. 1); see Castellanos et al. (1994) for a description of the site. Seeds were stored at 5 °C, under dry conditions and in darkness after harvest until the beginning of the experiment. Wrack was collected from the mean higher high water (MHHW) from the same marsh and it consisted of dead culms and leaves of different plant species (~50% of the debris was dead *S. densiflora*) together with pieces of shells (diameter < 1.0 cm). Collected wrack was checked for the presence of *S. densiflora* seeds and none was found, probably because seeds are dispersed before dead spiked shoots are transported by tides and currents.

### Wrack treatments

A greenhouse experiment was conducted from December 2009 to February 2010, since most *S. densiflora* seeds germinate during winter, to test the effects of wrack burial on seed germination, and emergence and growth of seedlings of *S. densiflora*. The mean disseminule size of *S. densiflora* was 9.67 ± 0.15 mm by 1.47 ± 0.02 mm (n = 50) and its mean weight was 3.0 ± 0.1 mg (range: 1.3-4.2 mg). Mean *Spartina* caryopsis size was 4.68 ± 0.08 mm by 0.98 ± 0.02 mm (n = 50) and its weight was 2.0 ± 0.1 mg (range: 1.3–3.0 mg). Four replicates of 25 seeds were sown at 1 cm depth in clean sand in plastic containers measuring 18 cm width, 22 cm length and 11 cm height (containing ~1.6 kg of clean sand). The sand was collected from the same marsh where the seeds were obtained and it was sieved through 0.5-mm mesh size filling to eliminate pre-existing seeds and other plant material. A control treatment was set up without any

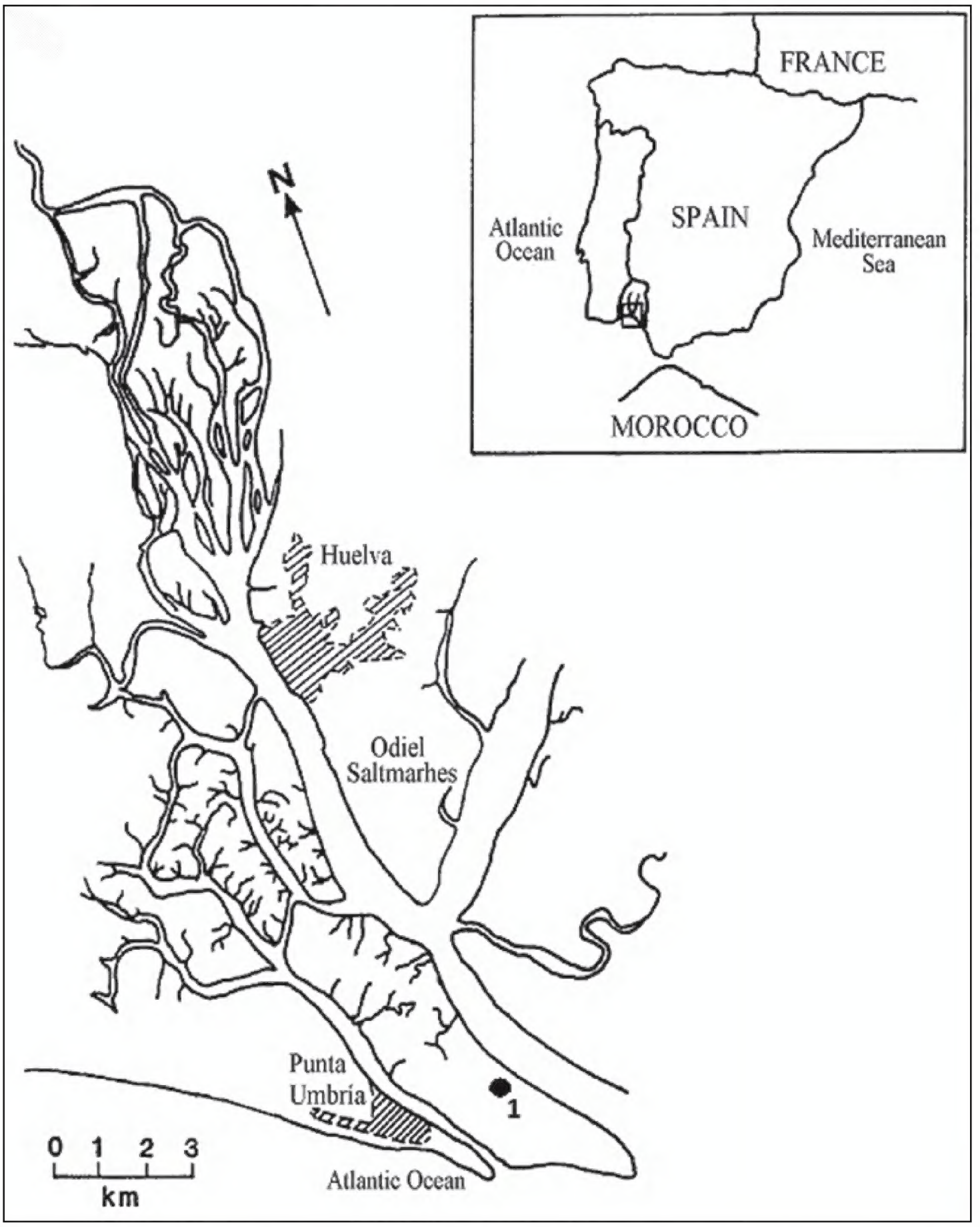


**Figure 1.** Location of the Odiel Marshes on the Atlantic coast of Southwest Iberian Peninsula (37°08'-37°20'N, 6°45'-7°02'W), and the sampling point where *Spartina densiflora* seeds were collected (1).

seeds added in order to test whether the sand we used contained seeds. Five wrack burial treatments were conducted: control (no wrack was added above the sand surface), 1 cm (1235 ± 92 g DW wrack $m^{-2}$), 2 cm (3266 ± 13 g DW $m^{-2}$), 4 cm (4213 ± 277 g DW $m^{-2}$), and 8 cm (6138 ± 227 g DW $m^{-2}$) of wrack burial depth. These treatments were decided following our field observations in Odiel Marshes (Southwest Iberian

Peninsula) where *S. densiflora* is very abundant (Nieva et al. 2001a). Each container had 25 seeds at one depth, so there were five treatments with four containers (replicates) per depth (n = 4 per treatment; n = 20, including all treatments together). Containers were irrigated gently once a day with water to ensure the moisture of the soil remained within 70% of its water-holding capacity. Fresh water (< 0.5 psu) was used to avoid salinity effects on germination since we wanted just to record seed responses to burial and avoid high salinity effects. *Spartina densiflora* is a facultative halophyte that can germinate, establish and develop in freshwater conditions (Nieva et al. 2001b; Castillo et al. 2005). The containers had small holes on the bottom to allow drainage, but these were covered with strips of cloth to prevent the loss of sand.

Sediment redox potential, electrical conductivity and pH were recorded at the end of the experiment in February 2010 at 1 cm depth in the sand. pH was recorded in the laboratory after adding distilled water to the soil (1:1, soil: distilled water, v/v) (pH/redox Crison with the electrode M-506). Soil salinity was measured as electrical conductivity (conductivity meter, Crison-522) after pH (1:2, soil: distilled water, v/v)). Redox potential was determined with a portable meter and electrode system in the greenhouse (Crison pH/mV p-506). Mean, maximum and minimum daily sediment temperature were recorded at 0, 1, 2, 4 and 8 cm depths using an electronic thermometer (SA880SSX, Germany) recording from 8 a.m. to 8 p.m. every 4 hours for 3 days ($n$ = 3). Average daily air temperature during the experiment was 18.5 ± 0.5 °C, varying between a mean low temperatures of 10.4 ± 1.6 °C and a mean maximum temperature of 34 ± 3.5 °C. Mean daily air relative humidity was 74.5 ± 2.6%, varying between 32.5 ± 5.5% and 92.5 ± 1.1%.

Emerged seedlings from beneath the wrack were counted every 24 h (Cui et al. 2007). The experiment continued until no additional emergence was observed during 10 days. At the end of the experiment, the wrack and the sand were carefully removed and those seedlings that died before raising the wrack surface were counted and ungerminated seeds were collected. At the end of the experiment, shoot and root length were measured on all seedlings and the number of roots counted. Germination percentage was calculated as the number of germinated seeds by the total number of seeds per treatment. Seedling emergence percentage was calculated as the number of seedlings raising above the wrack surface by the number of germinated seeds per treatment. Seedling aerial growth rate was recorded as the difference in emerged seedling height between two consecutive measures (in two days period) divided by the number of days.

Ungerminated seeds were transferred to 0.5-cm depth in sand and germination and emergence percentages were recorded until no more seeds germinated for 10 days. Germinated seeds were considered to be in a quiescent state, which is different than true seed dormancy and occurs when a seed fails to germinate because external environmental conditions are not appropriate (Baskin and Baskin 1985). Then, ungerminated seeds were soaked in water at 30 °C for 24 h. Seed coats were cut and the embryo was soaked in 1% tetrazolium chloride (Panreac Quimica S.A., Barcelona, Spain) for 24 h at 30 °C. Pink embryos were scored as alive and considered to be in dormancy (Baskin and Baskin 2004). Non-coloured seeds were considered to be dead. Quiescence, dormancy and mortality percentages were calculated in relation to the total number of seeds per treatment.

### Statistical analysis

Analyses were carried out using SPSS 12.0 (SPSS Inc, USA). Data were tested for homogeneity of variance and normality with the Brown-Forsythe test and the Kolmogorov-Smirnov test, respectively ($P < 0.05$). Plant traits were compared between treatments by one-way analysis of variance (ANOVA, *F*-test). Tukey Honest Significant Difference (HSD) test between means was calculated only if the *F*-test was significant ($P < 0.05$). The effect of wrack load on seedling growth rate between two treatments was analyzed using a Student *t*-test. Pearson correlation coefficient and linear regressions were calculated between abiotic factors, germination and seedling traits, and the wrack load. When a biotic characteristic was correlated with two or more abiotic environmental factors, multiple regression analysis was carried out to explore relative weights (β). Deviations were calculated as standard errors of the mean (SEM).

## Results

### Abiotic environment

Sediment pH increased with the wrack burial load from 6.2 ± 0.5 in the control treatment to 7.7 ± 0.1 under 8 cm ($r = 0.96$, $P < 0.01$, $n = 20$). Electrical conductivity changed from 0.11 ± 0.00 to 0.23 ± 0.00 mS $cm^{-1}$. Sediment redox potential varied between -83 ± 7 mV under 8 cm of wrack and +255 ± 5 mV without wrack burial (Table 1). Mean daily sediment temperature decreased at higher depths ($r = -0.61$, $P < 0.05$, $n = 20$), but without showing significant differences between treatments, varying between 12.3 ± 1.0 °C for the control treatment and 10.1 ± 0.8 °C at 4 and 8 cm (ANOVA, $F = 0.39$, $P > 0.05$). Maximum daily sediment temperature changed between +25.0 ± 0.8 °C for the control treatment and +21.7 ± 0.3 °C at 1 cm (ANOVA, $F = 2.02$, $P > 0.05$), decreasing also when wrack burial depth increased ($r = -0.36$, $P > 0.05$, $n = 20$). Minimum daily temperature varied between +10.4 ± 0.4 °C at 8 cm and +7.9 ± 1.0 °C for the control treatment (ANOVA, $F = 0.86$, $P > 0.05$), increasing with depth ($r = 0.81$, $P < 0.0001$, $n = 20$). Daily variation between maximum and minimum temperatures decreased at higher depths ($r = -0.62$, $P < 0.05$, $n = 20$), varying between 17.7 ± 1.4 °C for the control treatment and 12.4 ± 0.3 °C at 8 cm (ANOVA, $F = 2.46$, $P < 0.05$) (Table 1).

### Germination and establishment

The time to first emergence of *S. densiflora* was 23 days after the start of the experiment at control treatment and 37 days at 1 cm wrack depth. Germination decreased when wrack load increased ($r = -0.84$, $P < 0.0001$, $n = 20$), showing the highest value without wrack (96 ± 4%) and decreasing significantly under 8 cm deep (ANOVA, $P < 0.05$) (Fig. 2).

**Table 1.** Wrack load (g $m^{-2}$), sediment pH, redox potential (mV), electrical conductivity (mS $cm^{-1}$), daily mean, maximum and minimum sediment temperature (°C), and the difference between maximum and minimum temperature (°) ($n$ = 3) for five wrack burial depths. Different letters indicate significant differences between treatments (ANOVA, $P < 0.05$) ($n$ = 5).

| Wrack depth (cm) | Wrack load (g $m^{-2}$) | pH | Redox potential (mV) | Conductivity (mS $cm^{-1}$) | Daily sediment temperature (°C) | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | Mean | Maximum | Minimum | Max-Min |
| 0 | 0 ± $0^{a}$ | 6.2 ± $0.5^{a}$ | +255 ± $5^{a}$ | 0.23 ± $0.00^{a}$ | 12.3 ± $1.0^{a}$ | 25.0 ± $0.8^{a}$ | 7.9 ± $1.0^{a}$ | 17.7 ± $0.2^{a}$ |
| 1 | 1235 ± $92^{b}$ | 6.9 ± $0.3^{b}$ | +247 ± $2^{a}$ | 0.20 ± $0.02^{a}$ | 10.4 ± $0.9^{a}$ | 21.7 ± $0.3^{a}$ | 9.4 ± $0.5^{a}$ | 13.0 ± $0.3^{b}$ |
| 2 | 3266 ± $13^{c}$ | 7.1 ± $0.5^{b}$ | +229 ± $3^{b}$ | 0.16 ± $0.00^{b}$ | 10.2 ± $0.9^{a}$ | 22.5 ± $0.1^{a}$ | 9.7 ± $0.5^{a}$ | 13.1 ± $0.0^{b}$ |
| 4 | 4213 ± $277^{d}$ | 7.3 ± $0.1^{c}$ | +157 ± $11^{c}$ | 0.13 ± $0.01^{c}$ | 10.1 ± $0.8^{a}$ | 22.7 ± $0.8^{a}$ | 10.1 ± $0.4^{a}$ | 12.7 ± $0.1^{b}$ |
| 8 | 6138 ± $227^{e}$ | 7.7 ± $0.1^{d}$ | -83 ± $7^{d}$ | 0.11 ± $0.00^{d}$ | 10.1 ± $0.8^{a}$ | 22.5 ± $0.0^{a}$ | 10.4 ± $0.4^{a}$ | 12.4 ± $0.3^{b}$ |

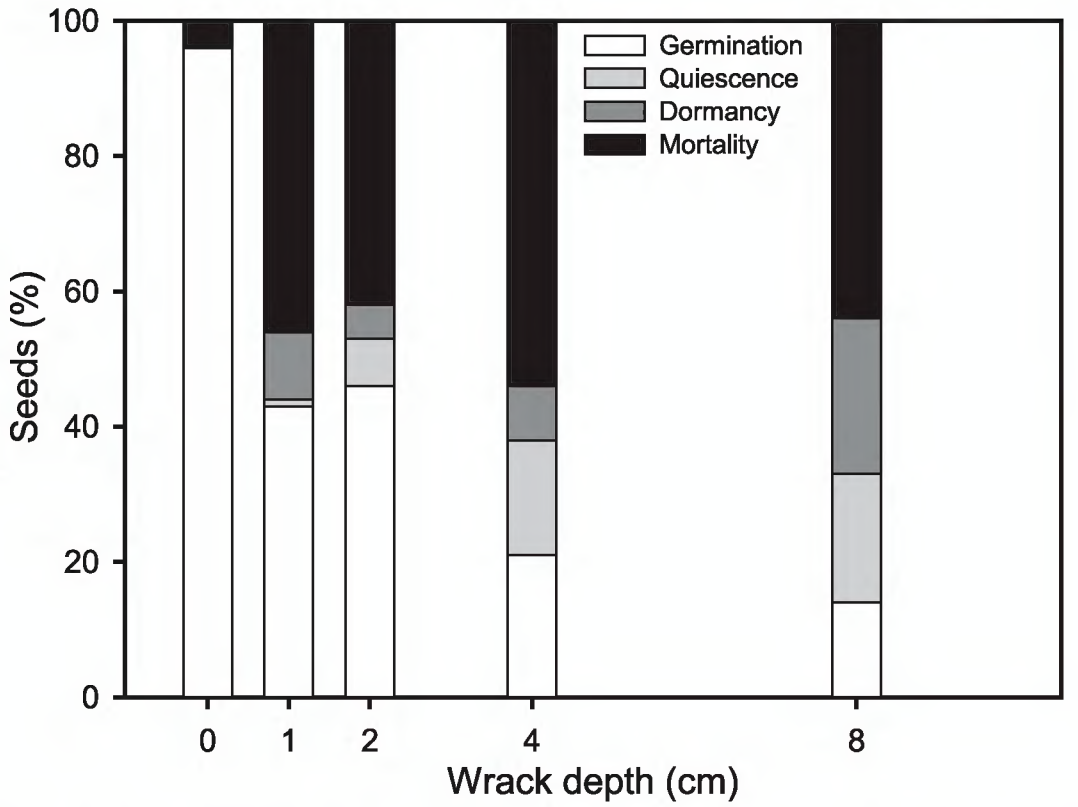


**Figure 2.** Germination, quiescence, dormancy and mortality of *Spartina densiflora* seeds for five wrack burial depths.

Germination percentage decreased at lower redox potentials ($r$ = 0.65, $P$ < 0.005, $n$ = 20; β = -0.599), varying from 96 ± 4% at the control treatment with sediment redox potential +255 ± 5 mV to less than 15% under 8 cm deep with negative redox potential -83 ± 7 mV. In addition, germination percentage increased at lower minimum daily sediment temperature ($r$ = -0.95, $P$ < 0.0001, $n$ = 20; β = -3.669) (Fig. 2).

Quiescence and dormancy percentages increased with wrack load ($r$ = 0.67, $P$ < 0.05, $n$ = 20; $r$ = 0.70, $P$ < 0.001, $n$ = 20, respectively). Quiescent percentage increased at higher minimum daily sediment temperature ($r$ = 0.57, $P$ < 0.05, $n$ = 20; β = 3.265) and at lower redox potentials ($r$ = -0.56, $P$ < 0.01, $n$ = 20; β = 0.495). No dormant seeds were recorded for the control treatment where seed mortality was the lowest (4%; 4 seeds). Dormancy and mortality increased to ~50% of the ungerminated seeds under wrack (Fig. 2). Dormant seed percentage and seed mortality increased mainly at higher daily minimum sediment temperature ($r$ = 0.70, $P$ < 0.001, $n$ = 20; $r$ = 0.81, $P$ < 0.0001, $n$ = 20, respectively).

No seedling emerged from deeper than 1 cm depth since every seedling died before emerging above the wrack surface. Minimum seedling mortality was recorded for the control treatment (7 ± 3% of germinated seeds) (ANOVA, $P$ < 0.05). The highest seedling emergence percentage occurred without wrack (93 ± 3%) and only 6 seedlings emerged from under 1 cm of wrack (11 ± 5%) (Table 2).

Seedlings in the control treatment were much taller and had longer and more roots than those growing from under 1 cm of wrack and also than those seedlings dying under the wrack at 2, 4 and 8 cm (Fig. 3). These results also showed a higher aerial growth rate for seedlings at the control treatment (0.11 ± 0.01 cm day$^{-1}$) than those growing from under 1 cm of wrack (0.02 ± 0.01 cm day$^{-1}$) ($t$-test; $P$ < 0.05).

**Table 2.** Emergence and mortality rates of germinated seeds for five wrack burial depths. Different letters indicate significant differences between wrack burial depths for the same trait (ANOVA, $P < 0.05$).

| Wrack depth (cm) | Emergence (%) | Mortality (%) |
|---|---|---|
| 0 | $93 \pm 3^{a}$ | $7 \pm 3^{a}$ |
| 1 | $11 \pm 5^{b}$ | $89 \pm 5^{b}$ |
| 2 | $0 \pm 0^{c}$ | $100 \pm 0^{c}$ |
| 4 | $0 \pm 0^{c}$ | $100 \pm 0^{c}$ |
| 8 | $0 \pm 0^{c}$ | $100 \pm 0^{c}$ |

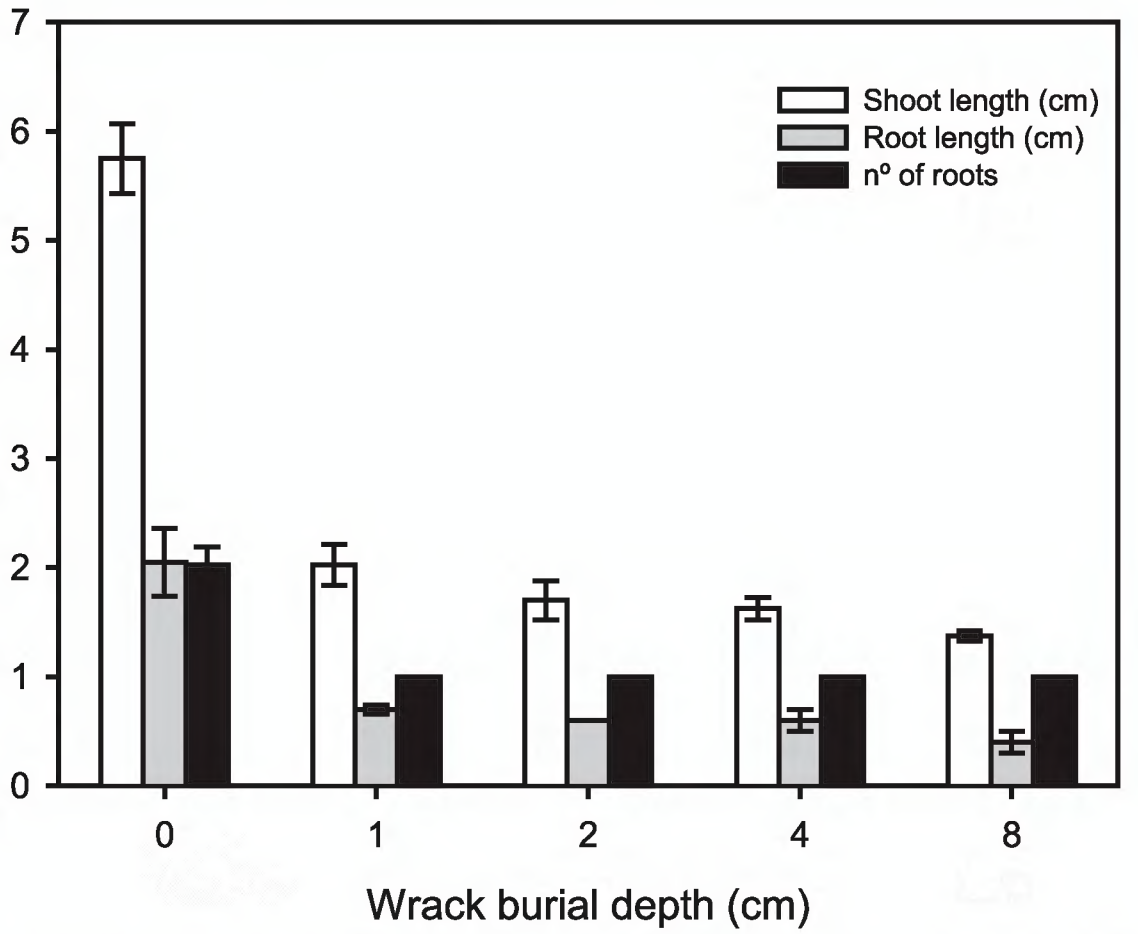


**Figure 3.** Shoot and root lengths (cm) and root number of *Spartina densiflora* seedlings for five wrack burial depths (seedlings from deeper than 1 cm were found dead and did not emerge above the wrack surface). Different letters indicate significant differences between wrack depths for the same trait (ANOVA, $P < 0.05$).

## Discussion

This study shows that germination and establishment of *S. densiflora*, an invasive cordgrass in Europe, North America and North Africa, is greatly limited by wrack burial.

Sediment pH increased with wrack burial load, which may be related to the presence of shells in the debris that would add carbonate to the sediment. However, *S. densiflora* germination would not be altered within the narrow recorded pH range (6.2–7.7) (Curado et al. 2010). Similarly, electrical conductivity varied within a range (0.11–0.23 mS $cm^{-1}$) that would not influence *S. densiflora* germination significantly (Castillo et al. 2005). In contrast, sediment redox potential under the debris may have affected germination under 8 cm of wrack since it was as low as -83 ± 7 mV, and germination decreased and quiescence increased at low redox potentials as it has been described previously in anaerobic environ-

ments under organic material in lakes (Rich and Wetzel 1978) and in accordance with our hypothesis. Negative values of redox potential can decrease *S. densiflora* germination in the field (Mateos-Naranjo et al. 2008). Sediment anoxia affects seeds by consuming oxygen resulting from degradation of organic matter (Wu et al. 2009). Thus, poor soil aeration may induce quiescence (Vleeshouwers et al. 1995).

The highest germination was recorded without debris (96%), decreasing markedly (to values between 21–43%) between 1 and 4 cm deep with positive redox potentials (> +150 mV). Therefore, other environmental factors in addition to anoxia seemed to be limiting *S. densiflora* germination under the debris. The effects of burial on germination can be mediated by changes in the light regime as it has been described for some halophytes (Pons 1992; Khan and Gul 2002), which is not the case for *S. densiflora* germination that is similar in light and darkness under fresh water conditions (Nieva et al. 2001b). However, synergistic effects between light and other abiotic factors cannot be excluded. Germination of *S. densiflora* increased at lower sediment daily minimum temperatures, conditions that were recorded without or under low loads of wrack, indicating that burial probably caused an unsuitable temperature environment for germination (Benvenuti et al. 2000). Thus, quiescence and dormant seed percentages increased at higher sediment minimum temperatures. In temperate regions, many grass species require exposure to low winter temperatures to come out of dormancy (Baskin and Baskin 1998). Sensitivity to temperature fluctuation functions as a depth- or gap-detecting mechanism; in this way, germination is activated when temperature fluctuation increases at unvegetated areas exposed directly to solar radiation (Thompson and Grime 1983). Furthermore, allelopathic effects from the plant debris inhibiting the germination of *S. densiflora* seeds cannot be excluded (Li et al. 2010; Sieg and Kubanek 2013).

*Spartina densiflora* did not show primary dormancy since all its seeds germinated or died (only 4%) without wrack in optimal conditions. Instead, *S. densiflora* seeds entered a non-deep physiological dormancy (Baskin and Baskin 1988) under the plant debris. Dormancy percentage increased with higher daily minimum temperature determining a lower daily temperature variation under the wrack. Secondary dormancy may be induced by environmental factors such as high $CO_2$ levels produced by debris decomposition (Harper and Obeid 1967), poor aeration (Simpson et al. 1989) and low temperature fluctuations (Baskin and Baskin 1998). Longer seed dormancy at greater depths within the debris would be ecologically advantageous because seeds would survive in the dormant state in the seed bank until the upper layer of wrack would be removed. Nevertheless, wrack burial increased seed mortality.

The establishment of *S. densiflora* seedlings was also greatly influenced by wrack. Only six seedlings emerged above the plant debris from a burial depth of 1 cm, while no seedling emerged from deeper than 1 cm (wrack load > 3 kg DW $m^{-2}$). The seedling of *S. densiflora* has just one thin and sharp cotyledon that grows easily along an axis, being able to emerge straight away from 4 cm depth in water (Abbas et al. 2012) and in sand (A.M. Abbas, personal observation). In contrast, when a seedling grew within wrack it had to find the few hollows left open in the wrack as is reflected in its cotyledon growing in curves. Every *S. densiflora* seedling dying within the debris was shorter

than 2 cm, which seemed to be the longest length they were able to grow under these conditions. The dense structure of the debris would prevent *Spartina* from emerging from deeper than 1 cm due to the exhaustion of food reserves before getting to the surface (Martínez et al. 1992; Bond et al. 1999). It has been previously described how deeply sown seedlings in sediment died before emerging in wetlands (Hartleb et al. 1993; Jurik et al. 1994; Wang et al. 1994; Dittamar and Nelly 1999; Spencer and Ksander 2002; Ke and Li 2006). Live and dead standing biomass of *Spartina patens* (Aiton) Muhl prevented seedling emergence of subordinate annuals and perennials in coastal marshes (Brewer and Grace 1990; Baldwin et al. 1996). *Spartina densiflora* seed germination and quiescence presented a gradual response to wrack burial but seed dormancy, seed and seedling mortality and seedling emergence showed a threshold dynamic in response to wrack burial, increasing markedly even under just 1 cm depth. These results characterized *S. densiflora* as a very sensitive species to wrack burial during the establishment period, which may limit its invasion in those marshes accumulating high debris loads.

*Spartina densiflora* seedling development was also significantly reduced by wrack burial. Seedlings growing without wrack were ~5.8 cm tall at the end of the experiment while seedlings emerging from 1 cm deep under the wrack were ~2 cm tall (including their buried part), coinciding with lower growth rates. In adittion, seedlings in the control treatment had longer and more roots. In this sense, it has been reported that phytotoxins generated in anaerobic decomposition can inhibit the growth of freshwater plants (Barko and Smart 1986; Maun and Lapierre 1986).

Our experimental results are in accordance with our field observations. In tidal salt marshes, wrack is accumulated mainly coinciding with the mean higher high water. We have observed in the field (Odiel Marshes) that the wrack depth in these areas ranges from 2 to 14 cm. In these marshes, we have seen no *S. densiflora* seedling growing from within the wrack. Just very few *Spartina* adult clumps were observed within the debris areas, which seemed to have established before wrack accumulation or within open patches in the wrack. *Spartina densiflora* tussocks accumulate high densities of dead tillers in middle and high marshes (Nieva et al. 2001a) and when this necromasa is detached from the tussocks is accumulated as wrack. In view of our results, as *S. densiflora* invades a location it would decelerate its own invasion rate through the accumulation of wrack that may limit its establishment.

## Conclusions

Data gathered during this study confirmed an inverse relationship between germination and emergence with wrack burial for the invasive cordgrass *S. densiflora*. Germination decreased from 96% without wrack to 14% at 8 cm deep in debris (ca. 6 kg DW $m^{-2}$). No seedling emerged above the wrack surface for seeds germinated at wrack burial depths greater than 1 cm (a wrack load of ca. 1 kg DW $m^{-2}$). The results from this study improved our understanding of *S. densiflora* invasion and they are useful

to predict invasion dynamics and to plan the management of invaded marshes. Thus, wrack may be used to limit *S. densiflora* colonization and should not be removed from those areas sensible to the invasion of this cordgrass.

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